

Early Lycophyte Evolution

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ABSTRACT.—Lycophytes, comprising the groups historically known as the lycopsids and zosterophylls, have the longest history of any group of vascular land plants. The early evolution of the group is reviewed concentrating on the Late Silurian and Devonian record of Lycopsidea and Zosterophylloids. Distinct root-like and shoot-like axes in zosterophylloids and lycopsids are first recorded in the Early Devonian and can be compared to the later development of pseudobipolar growth of tree-shaped lycopsids with upward-growing trunks and branch systems and downward-growing rooting systems. The development of stigmarian rootlets postdates the evolution of pseudobipolar growth, first recorded in the Middle Devonian, according to current evidence. Other important events in early lycophyte evolution during the Devonian include changes in leaf morphology, modification of sporophylls, and the eventual appearance of the lycopsid strobili.

WHAT IS A LYCOPHYTE AND WHEN DID LYCOPHYTES APPEAR?

The lycophytes (= club mosses and related plants) are regarded as a distinct lineage of vascular plants with a long evolutionary history. Considerable diversity is evident for much of their existence, although only four (or 7+ if one accepts either Øllgard's (1987) or Wagner and Beitel's (1992) splitting of *Lycopodium* into several genera) herbaceous genera are recognized today (*Lycopodium* (and segregates), *Phylloglossum*, *Selaginella*, and *Isoetes*). Club mosses have long been defined as plants with microphyllous leaves, axillary or adaxially borne reniform sporangia with dehiscence along their distal margin, and mostly exarch xylem maturation; such plants are now included in the class Lycopsidea ("lycopsids") by Kenrick and Crane (1997). Extinct taxa attributed to Zosterophylloids (and possibly including barinophytes) are considered closely related to lycopsids, either as ancestral or sister taxa (Gensel, 1992; Hueber, 1992; Bateman, 1992; Kenrick and Crane, 1997), being similar in sporangium shape and xylem attributes but differing from lycopsids in lacking leaves and leaf-borne sporangia. Additionally they have vascularized sporangial stalks (Fig. 1).

REDEFINITION OF "LYCOPHYTES" AND "LYCOPSIDS".—Several workers emphasize the monophyly of vascular plants (Mishler *et al.*, 1994; Stewart and Rothwell, 1993; Kenrick and Crane, 1997). Many types of evidence, molecular and morphological, demonstrate that lycophytes *sensu lato* form a distinct lineage of vascular plants from early in their evolutionary history (Raubeson and Jansen, 1992; Kranz and Huss, 1996; Kenrick and Crane, 1997). In Kenrick and Crane's recent, extensive morphological phylogenetic analysis of living and extinct plants, monophyly is supported, and zosterophylls and lycopsids are interpreted as two classes in a larger group, subdivision Lycophytina (Fig. 1). This

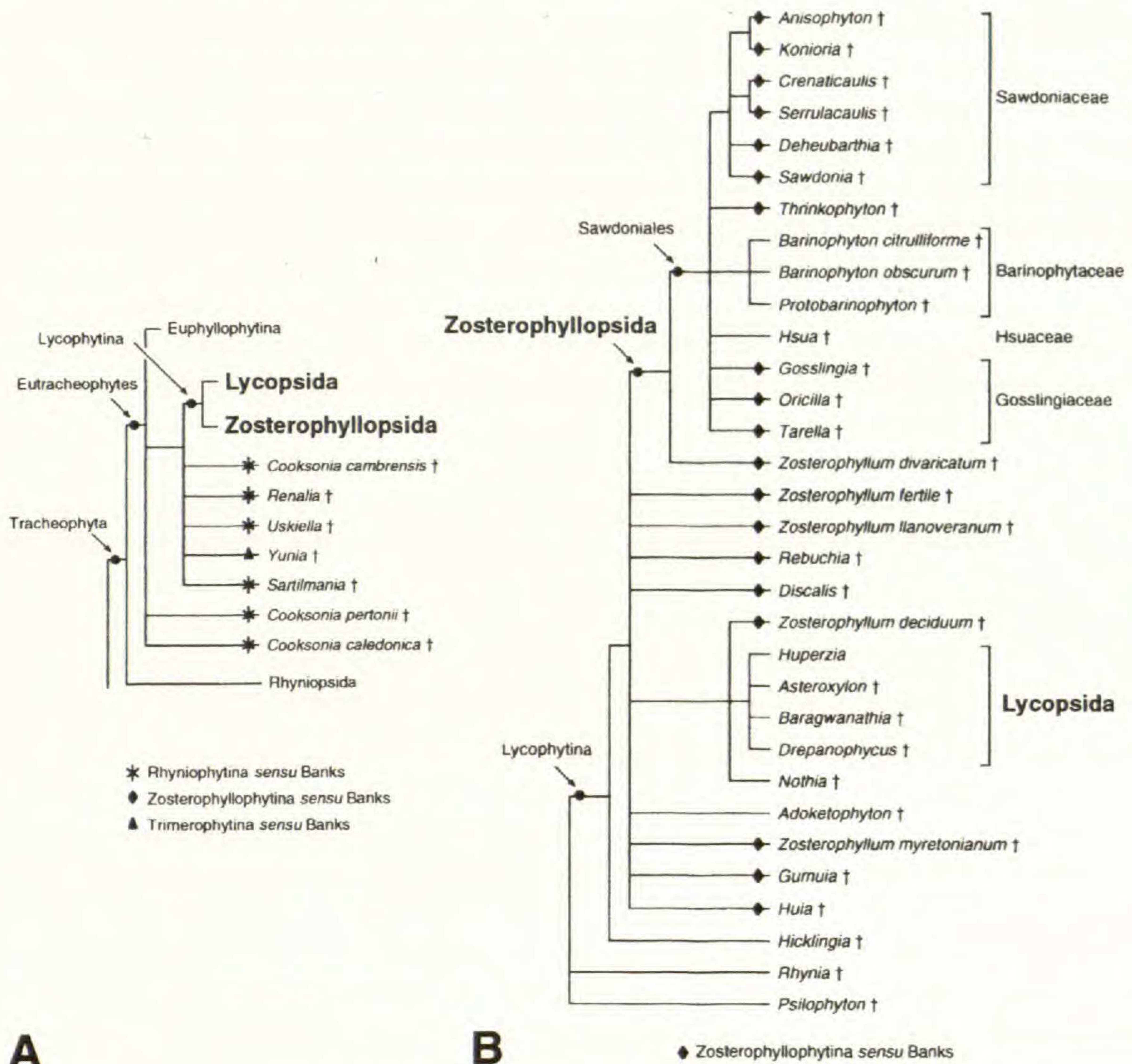


FIG. 1. Strict consensus trees showing relationships among several polysporangiophyte taxa and among lycophytes according to analyses conducted by Kenrick and Crane (1997). A) Adapted from Kenrick and Crane, fig. 4.31. B) From Kenrick and Crane, fig. 5.25, with permission. Zosterophylloids and Lycopsida are highlighted. See text for discussion. Not all taxa discussed in the text are included, partly because of differences in preservation and therefore absence of characters for some taxa.

larger group is defined (p.237–238) by the following synapomorphies: “more or less reniform sporangia, marked sporangium dorsiventrality, isovalvate dehiscence along distal sporangium margin, conspicuous cellular thickening along sporangial dehiscence line, sporangia on short, laterally inserted stalks, exarch xylem differentiation.” Within the Lycophytina, the strict consensus tree of their analysis (p. 172) shows a polytomy (Fig. 1B) from which emerge the Zosterophylloids, a clade largely consisting of lycopsids, and a large number of individual taxa. Zosterophylloids sensu Kenrick and Crane (Fig. 1B) are defined by only two synapomorphies, namely circinate growth and a unique, two-rowed arrangement of sporangia. Among the single unresolved taxa excluded from Zosterophylloids sensu stricto are several plant genera (*Rebuchia*, *Discalis*) originally placed among the zosterophylls, several species

of *Zosterophyllum* including the type species (*Z. myretonianum* Penhallow), and some recently discovered Chinese forms. Thus Kenrick and Crane regard plants traditionally considered zosterophylls as paraphyletic. The incomplete data among the taxa analyzed for all characters employed, and lack of resolution at lower levels in the cladogram, indicates further investigation of characters and character homologies is needed. Thus these conclusions should be regarded with caution until additional data are available.

Kenrick and Crane (1997) define the second clade, the Lycopsidea (Fig. 1B), by the synapomorphies of microphylls, stellate xylem strand, vascularized leaves, sporophylls (close association of sporangium and leaf), and loss of sporangial vasculature. Lycopsidea includes a clade composed of three possibly transitional genera, *Asteroxylon*, *Drepanophycus*, and *Baragwanathia*, and a second larger clade of plants traditionally considered as lycopsids. The first clade is composed of taxa that do not possess all of the characters definitive of lycopsids—*Asteroxylon* and *Drepanophycus* have cauline sporangia with a vascularized stalk, and *Asteroxylon* lacks full vascularization of lateral appendages. Neither has a sporangium associated with a leaf, as occurs in members of the lycopsid clade and most probably in *Baragwanathia* (Hueber, 1992).

TIME OF APPEARANCE.—The occurrence of the genus *Baragwanathia* in the presumed late Silurian (Ludlow; Garratt *et al.*, 1984; Rickards, 2000) of Victoria, Australia suggests a possible pre-Devonian diversification of lycophytes. Zosterophylls also are recorded from these strata, but detailed descriptions are lacking (Tims and Chambers, 1974). Most other occurrences of late Silurian plant remains are much smaller in size and simpler in organization than either *Baragwanathia* or *Zosterophyllum* (Fig. 2). An interesting exception is the assemblage of zosterophylls and related plants from well-dated late Ludlow strata of Bathurst Island (Kotyk *et al.*, in prep.). These new forms support an early diversification of the lycophyte lineage.

POSSIBLE PRECURSORS.—Most polysporangiate plants (i.e. plants with branched sporophytes) with round to reniform sporangia referred to either as rhyniophyte?, cooksonioid, or rhyniophytoid (Taylor, 1988; Hueber, 1992) represent possible close relatives or precursors to the lycophytes but currently there are no obvious candidates. Outline drawings (Fig. 2) of several Late Silurian and Early Devonian rhyniophytoids show that these plants mostly are very small and exhibit variable sporangial shapes and modes of dehiscence. Their small size, simple construction, lack of anatomical preservation, and fragmentary preservation make more precise inference impossible, but those with globose-reniform sporangial construction may represent likely candidates for lycophyte precursors. A few larger forms with similar sporangial morphology have been recorded in pre-Devonian or earliest Devonian deposits, such as the specimen from the Ludlow of Bathurst Island (Basinger *et al.*, 1996; Kotyk, 1998) which resembles a pseudomonopodial *Cooksonia* or very simple *Zosterophyllum* (fig. 2 I).

Renalia, and some *Cooksonia* species, inferred to have arisen from within the plexus of latest Silurian-earliest Devonian rhyniophytoids (but their rela-

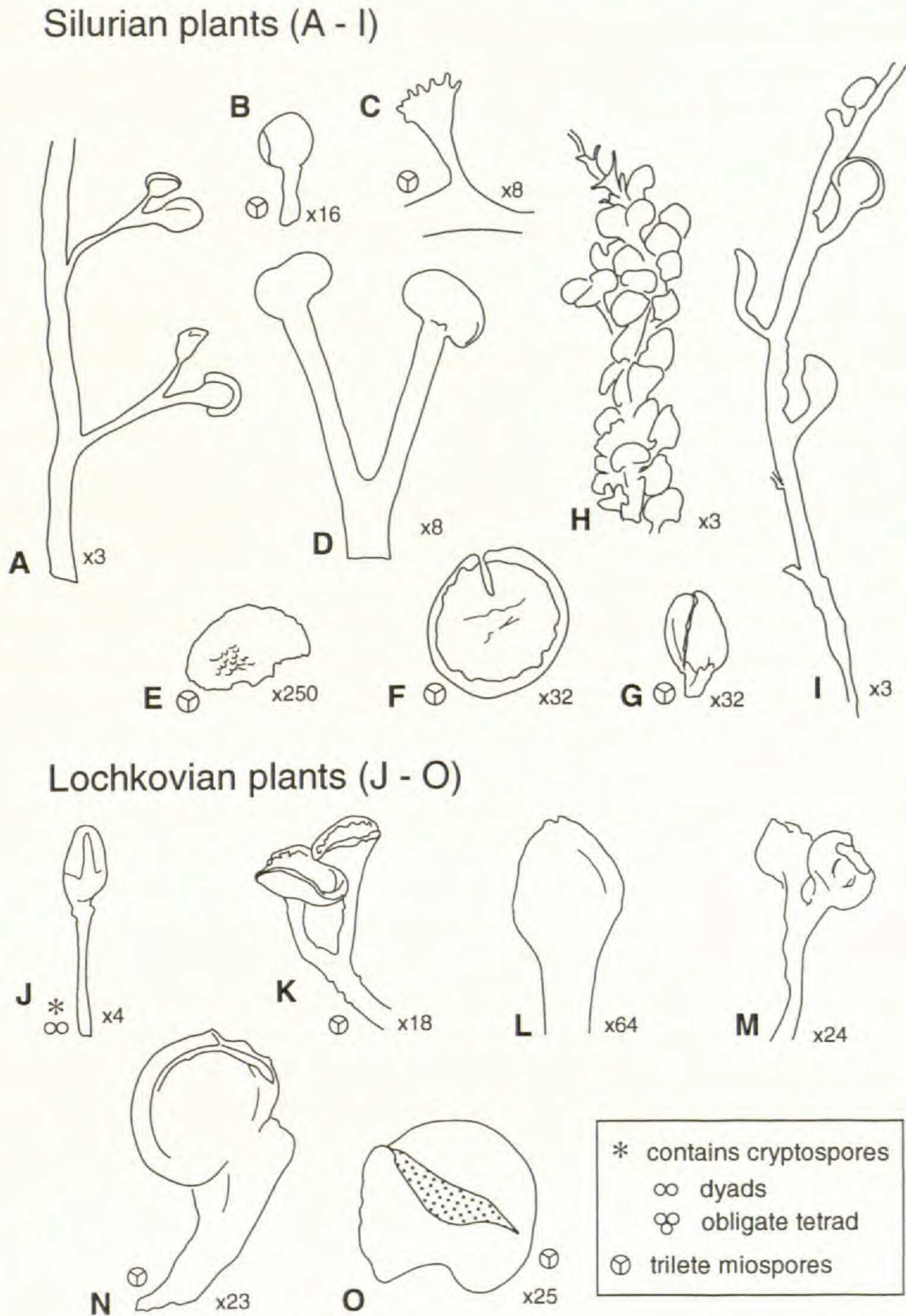


FIG. 2. Selected late Silurian and earliest Devonian meso- and megafossils. A—I) Pridoli plants. A) from Cai *et al.* (1993); B—D) from Fanning *et al.* (1991); E—G) from Edwards (1996). H) from Kotyk (1998). I) from Basinger *et al.* (1996). J—O). Lowermost Devonian plants from Edwards (1996).

tionship to these simple plants thus far is not extensively tested by cladistic analyses), also represent likely precursors. When *Renalia* and *Cooksonia* were included in the phylogenetic analyses of Kenrick and Crane, they formed part of the large basal polytomy of the polysporangiophytes and were interpreted as possible stem-lineage zosterophylls. Further investigation of these early plants is needed.

The present contribution notes major advances and addresses several areas of concern in regard to early lycophyte evolution and diversification, including current views of zosterophylls, early lycopsids, and evolution of major lycophyte structures.

CURRENT DATA ON ZOSTEROPHYLLS

As a probable sister group(s) or stem group(s) to lycopsids, zosterophylls *sensu lato* (Fig. 3A–3C) may provide evidence of early evolutionary patterns within these lineages. However, presently recognized taxa, while demonstrating greater diversity of form and some new combinations of characters, do not alter conceptions of relationships between zosterophylls and lycopsids nor aid in clarifying ordinal or familial delimitation within zosterophylls. The two main zosterophyllopid clades *sensu* Kenrick and Crane (1997) can be typified by two genera, *Sawdonia ornata* (Fig. 3A) and *Oricilla bilinearis* (Fig. 3C). Differences include sporangium orientation and presence/absence of emergences (multicellular appendages). The *Sawdonia* clade (Kenrick and Crane's Sawdoniaceae) exhibits more upright orientation of sporangia and emergences of varying morphology and arrangement, while the *Oricilla* clade (Kenrick and Crane's Gosslingiaceae) exhibits naked axes and sporangia stalks attached perpendicular to the axis. The *Zosterophyllum* depicted in Fig. 3B exhibits helically arranged sporangia and is most similar to those species of *Zosterophyllum* that form part of the basal polytomy in Kenrick and Crane's analyses. Beyond these two well-supported clades, we now have considerable new information about some of the more basal lineages, discussed next.

Plants which appear very similar to *Zosterophyllum* (Fig. 3B), except that sporangia are more scattered and borne on longer stalks than in many previously described *Zosterophyllum* species, are found in Pragian deposits of China and Bathurst Island, Canadian Arctic Archipelago (Kotyk, 1998). These do not quite fit existing generic or species delimitations, but as they become more completely known, they might aid in a better understanding of the genus *Zosterophyllum* or closely allied taxa. The separation of several *Zosterophyllum* species into separate clades in Kenrick and Crane's analysis is based mostly on symmetry of sporangial arrangement and presence/absence of circinate vernation. However, these characters are not easy to evaluate and their coding may not reflect that data about them are incomplete; most particularly, several taxa lacked anatomy. It is difficult to document the presence or (known) absence of circinate vernation (and true terminations). The character "symmetry of sporangial arrangement" may be difficult to ascertain because determining if sporangia are helically arranged or are subopposite in two rows is difficult in compression remains. A two-rowed pattern could be produced by a widely spaced, very simple helix coupled with twisting of either sporangial stalks or the axis (see Gerrienne, 1996b for an analysis of this feature). Current analyses indicate these new *Zosterophyllum* species and other *Zosterophyllum*-like plants may represent stem zosterophylls for which only a few distinguishing characters are present.

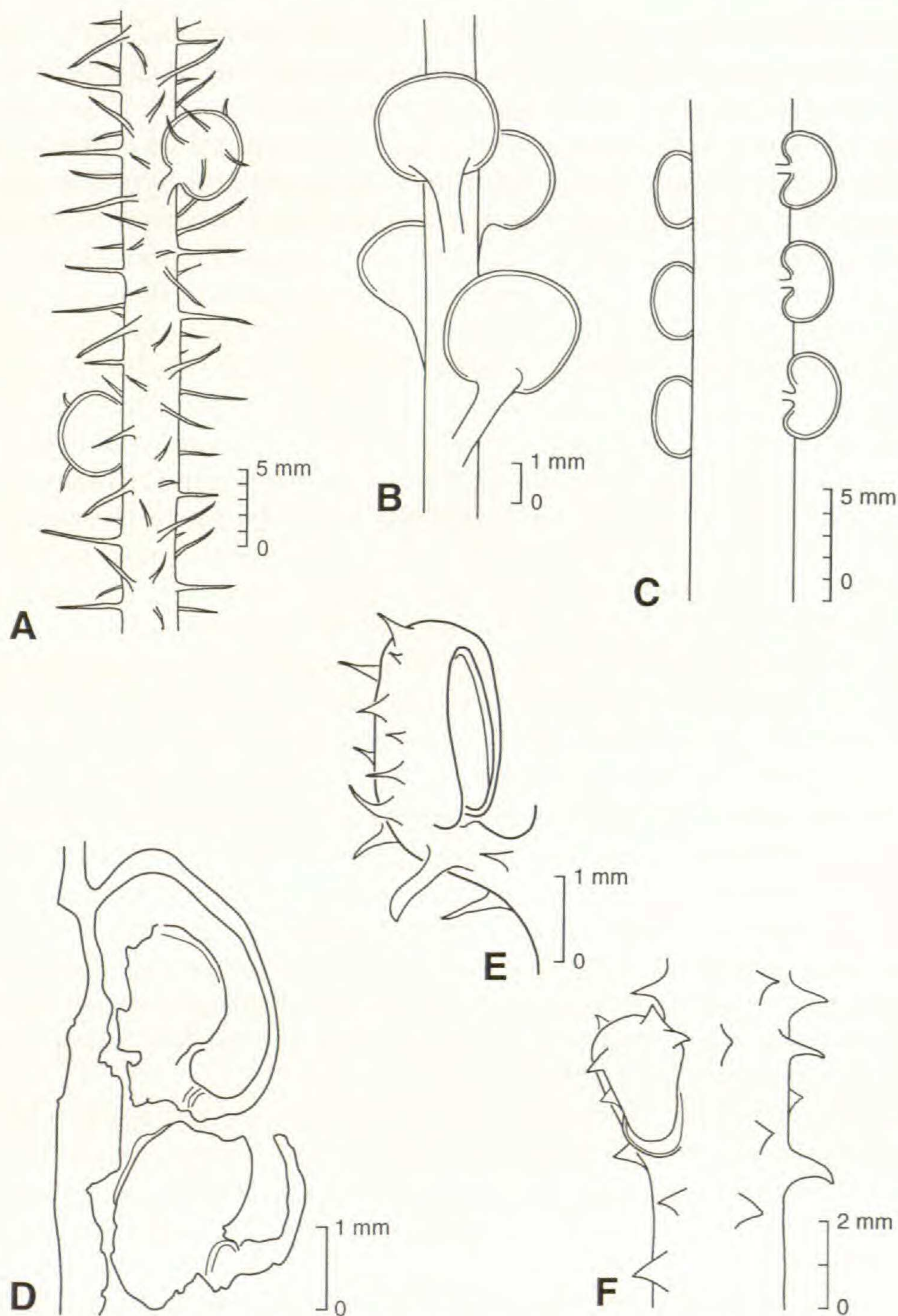


FIG. 3. Selected putative basal lycophytes or zosterophylloids. A, C) Representatives of Zosterophyllopsida *sensu* Kenrick and Crane. A) *Sawdonia ornata* (Dawson) Hueber, based on specimens from Gaspé. C) *Oricilla bilinearis* Gensel, redrawn from Gensel (1982). B) Depiction of a *Zosterophyllum* with helically arranged sporangia, a stem group taxon according to Kenrick and Crane (1997). D) *Gosferia curvata* Gerrienne from the Early Devonian of Belgium. Note thickening near base of sporangium. Redrawn from Gerrienne (1991). E) *Ensivalia deblondii* Gerrienne, a probable zosterophyllopid from the Early Devonian of Belgium. F) *Faironella valentula* Gerrienne, affinity uncertain, from the Early Devonian of Belgium. Sporangium is borne inside a recurved, thickened spiny structure. E, F) redrawn from Gerrienne (1996).

Another possible basal taxon, *Gosferia curvata* Gerrienne (1991, 1999), from the Early Devonian of Belgium, is unique in having long, basipetally recurving stalks, each terminated by a reniform sporangium (Fig. 3D). The closest similarity of this plant is to some unidentified zosterophyll-like plants in China and Bathurst Island and to some Silurian-Pragian rhyniophyte-like plants. The occurrence of a swelling near the sporangium base where it attaches to the stalk also is of interest; similar swellings are known in some *Drepanophycus* species (Li and Edwards, 1995) and in *Kaulangiophyton* (Gensel, pers. obs.). What it represents in any of these plants is currently unknown (but see below).

Ensivalia deblondii Gerrienne (1996a) from the Early Devonian of Belgium has spiny, anisovalvate sporangia terminating stout stalks. The abaxial sporangial valve is enlarged and spiny, inside of which the more delicate, smooth adaxial valve rests (Fig. 3E). *Odonax borealis* Gerrienne (1996b), also from Belgium, and some unnamed zosterophylls from the Early Devonian of New Brunswick also exhibit modification of the sporangium/stalk in the form of enlargement of either stalk or distal sporangium valve and presence of emergences, features which perhaps help protect the sporangium.

Further evaluation of the variability of emergence types (see Gensel, 1992 and Kenrick and Crane, 1997 for examples) among zosterophylls is needed as well as, perhaps, clarification of the homologies of different types of emergences. For example, in *Nothia aphylla* (Lyon, 1964) El Saadawy and Lacey (1979), the so-called emergences are produced by raised areas of axial tissue (cortex and epidermis), resulting from expansion of existing cells, with apically located stomata (Kerp *et al.*, 2001). Are these structures truly emergences or do they represent short, discontinuous ridges of the stem? The unusual prismatic emergences of *Serrulacaulis* (Berry and Edwards, 1994) and those now known to occur in *Bathurstia* (Kotyk and Basinger, 2000) also add to diversity of those structures but do not provide any further tests of homology between emergences and microphylls.

Some Early Devonian plants in which sporangia are arranged in an obvious strobilus may relate to the lycophyte clade, either among zosterophylls or lycopsids. *Demersatheca*, based on only a few leafless fertile specimens from the Pragian of China, exhibits reniform sporangia deeply sunken into the axis (Fig. 4D) and forming tight strobili (Li and Edwards, 1996). Other plants with strobili include *Distichophytum* and *Bathurstia*, both attributed to the zosterophylls, and some un-named plants of uncertain affinity from Bathurst Island. This morphology blurs the distinction between zosterophyll and barinophyte to some extent.

Barinophytes are defined, according to Kenrick and Crane, by a very compact, unbranched strobilus, indehiscent sporangia, intrasporangial heterospory, and sporangia borne on a horizontally extended axis which wraps around the stem (their "clasping" sporangium orientation). However, their relationships are unclear as the Barinophytaceae form part of a polytomy that includes some major groups of zosterophylls in Kenrick and Crane's analysis. More data are needed about sporangium shape, attachment, and dehiscence in both the early strobilate plants and some plants usually attributed to barinophytes, such



FIG. 4. Plants from the Pragian of China that may be related to lycophytes. A) *Adoketophyton subverticillatum* Li and Edwards with a leaf-like appendage subtending each sporangium. Redrawn from Li and Edwards (1992). B, C) *Eophyllophyton bellum* Hao, in which lobed leaf-like structures terminate lateral axes. Globose to reniform sporangia attach on the upper surface of the lobes. Redrawn from Hao and Beck (1993). D. *Demersatheca contigua* Li and Edwards, with sporangia sunken in the axes. Redrawn from Li and Edwards (1996).

as *Protobarinophyton*. *Faironella valentula* Gerrienne (1996a) is also of interest in this discussion as a possible link between zosterophylls and barinophytes. Its sporangia are attached to the inside of a curved appendage (Fig. 3F), and while affinities presently are uncertain, it thus bears some resemblance to Barinophytaceae.

Adoketophyton, a genus described from the Pragian of China by Li and Edwards (1992), demonstrates fertile regions with leaf-like structures that bear sporangia in their axils (Fig. 4A). Crane and Kenrick (1997) suggest the leaf-like structures might represent sterilized sporangia that became modified as a "leaf" as a result of changes in developmental processes such as multiplication and co-option. Another plant from the Pragian of China, *Eophyllophyton bellum* (Hao) Hao and Beck (1991) has the habit of a typical Early Devonian plant, but bears lobed, laminate leaf-like structures (Fig. 4B, 4C). Whereas this plant is at the base of the euphyllophyte clade of Kenrick and Crane, largely because



FIG. 5. Line drawing of *Drepanophycus qujingensis* Li and Edwards. Note cauline sporangia not associated with leaves. Redrawn from Li and Edwards (1995).

of its centrarch protostele, its globose-reniform sporangia are located adaxially on leaves and its tracheids possess G-type wall thickenings like those present in many zosterophylls and stem-lycophytes. In our opinion, this plant possesses an odd suite of characters for basal euphyllophytes and it is perhaps more appropriately considered in the context of zosterophylls or lycopsids. Both *Adoketophyton* and *Eophyllophyton* thus provide idiosyncratic evidence of the development of laminate appendages, but little information on their homologies.

PRE-LYCOPSIDS

This term has been applied to plants with many lycopsid characters, but lacking the consistent association of sporangium with a leaf or lacking fully vascularized leaves. Genera included are *Drepanophycus*, *Kaulangiophyton*, *Asteroxylon*, and in some instances, *Baragwanathia* (for another interpretation, see Hueber, 1992). They form a sister clade to other lycopsids in Kenrick and Crane's analysis and are treated there as a stem-based group of Lycopsida, the Drepanophycales. However, some aspects of their structure remain controversial, and re-evaluation of these features may influence their position relative to lycopsids or the interpretation of their evolutionary significance.

Based on current knowledge of *Drepanophycus*, the following appears certain: two species of *Drepanophycus*, *D. qujingensis* Li and Edwards and the type species *D. spinaeformis* (Goeppert) Li, Hotton and Hueber, exhibit both rhizomatous and aerial axes covered with vascularized microphyllous leaves and cauline sporangia (Fig. 5; Li and Edwards, 1995; Li *et al.*, 2000). Among

vegetative remains assigned to *Drepanophycus*, leaf morphology varies considerably, from long and falcate to short and thorn-like. It has been suggested that the axes with the former represent aerial regions, those with the latter rhizomatous axes. Sporangia borne on comparatively short stalks (usually shorter than leaves) are interspersed among the microphyllous leaves, with no apparent association with them.

Kaulangiophyon akantha exhibits a similar growth habit to that of *Drepanophycus*, but with all axes covered in stout, thorn-like emergences (Gensel *et al.*, 1969). Studies are underway to test assertions that *Kaulangiophyton* is very similar to or congeneric with *Drepanophycus* (Kasper, 1972; Schweitzer and Giesen, 1980), or that *Kaulangiophyton* has sporangia associated with leaves (Hueber, 1992). Careful examination of original Maine collections and new material from New Brunswick shows no indication of vascularization in the emergences. Sporangia were originally described as cauline, terminating a moderately long stalk and extending beyond emergences (Gensel *et al.*, 1969). Hueber (1992) noted features of the sporangial stalk that led to his hypothesis that a leaf extends beneath the sporangium but is obscured by the sporangium and thus is not visible on impression remains. We note that the stalks of some sporangia attach to a thickened pad or ring of coalified material that itself is borne on an axial protrusion. It resembles the pad at the base of sporangia in *Stockmansella* and *Huvenia*. A similar thickening may occur in *Drepanophycus qujingensis*. However, in contrast to Hueber's ideas, no extra appendage, emergence, or leaf lamina has been demonstrated in attachment to this thickening in *Kaulangiophyton*. Additional information on these and other characters of *Kaulangiophyton* and assessment of relationships will be presented in a later paper.

ROOTING STRUCTURES IN EARLY LYCOPHYTES

Information about rooting structures, other than rhizoids, in basal lycophytes is increasing, being recorded for the zosterophylls *Zosterophyllum*, *Bathurstia*, *Crenaticaulis* (Gensel *et al.*, 2001), and *Hsua* (Li, 1992), for *Drepanophycus* (Rayner, 1984; Li and Edwards, 1995; Gensel *et al.*, 2001) and for the rhyniacean *Stockmansella* (*Taeniocrada*) *langii* Fillion-Demaret (1985) by Schweitzer (1980). Two patterns are recognized by Gensel *et al.* (2001) and may correlate with habit. The first pattern occurs in tufted forms, such as some *Zosterophyllum* species, which produce downward trending axes from a central region that appear root-like. Upward trending axes departing from the same point are interpreted as shoots. In the other pattern, slender smooth axes depart from the rhizomatous regions, and in some cases divide to varying degrees. These frequently lie across, not on, the bedding plane. Also, they are sometimes produced during the formation of K-branches as in *Bathurstia* and *Drepanophycus* (Gensel *et al.*, 2001). In these plants, an axis departs, then forks. One of the resultant axes is oriented towards the rhizome apex and appears identical to shoots and the other, lacking either emergences or leaves and directed away from the apex, appears root-like (Figs. 6A, 6B). Based on

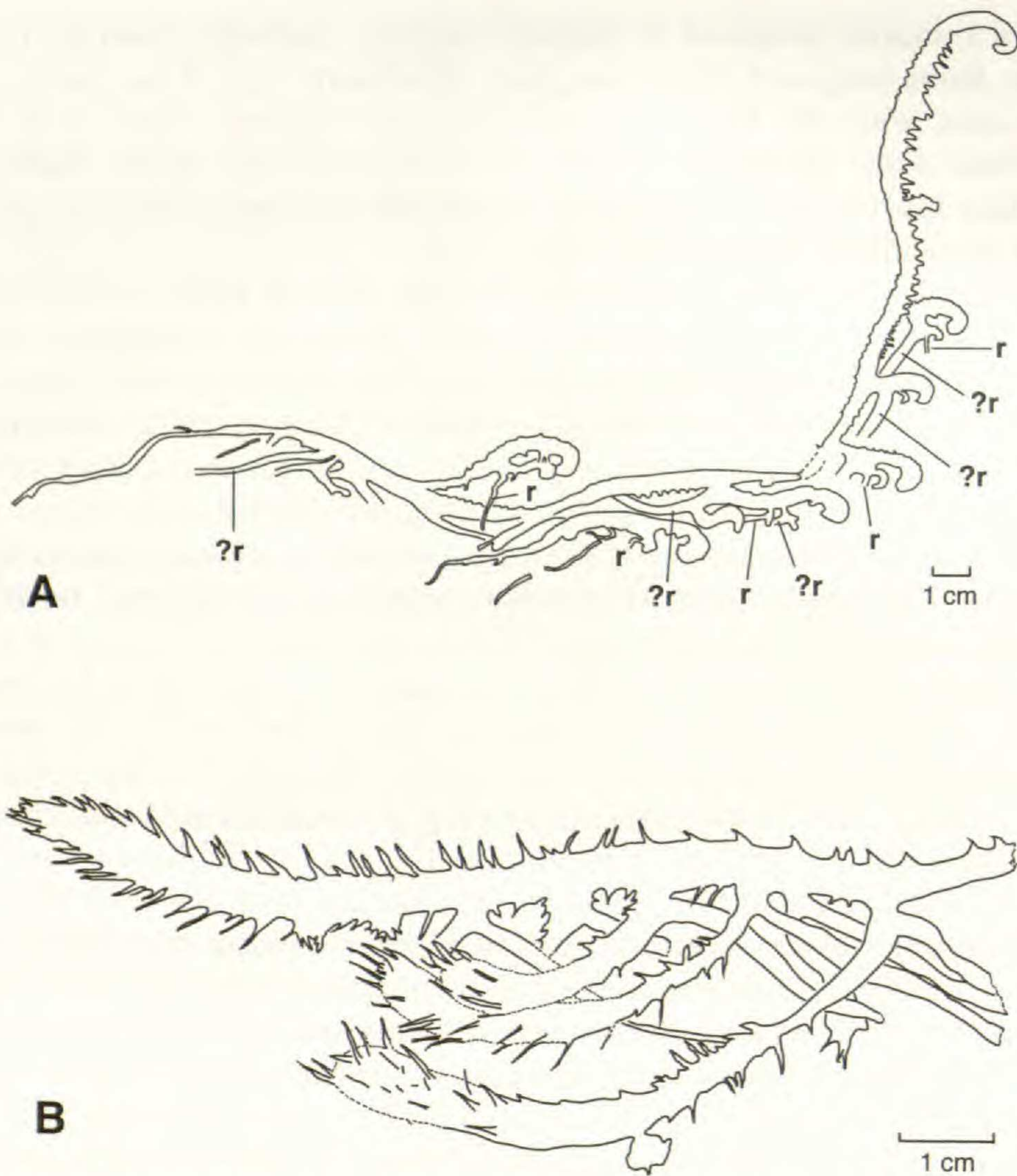


FIG. 6. A) Line drawing of the zosterophyll *Bathurstia denticulata* (Hueber) Kotyk and Basinger, showing numerous K-branches in which one portion is a rooting structure and the other a shoot-like structure, frequently in crozier form. B) Line drawing of *Drepanophycus* from the Pragian of Bathurst Island, showing several K-branches in which one part is a shoot and the other a smooth, root-like organ. r = rooting organs. Redrawn from Kotyk (1998), with permission and Gensel et al. (2001).

current evidence, these rooting structures appear to be similar and perhaps homologous to shoots. Gensel *et al.* (2001) postulate that among lycopsids, and perhaps most non-seed plants, roots arose via a dichotomy of the shoot system, with one apex transformed into a root apex. This condition occurred over time progressively earlier in ontogeny, until the root arose in the embryo. The position of the root primordium lateral to a shoot apex in many pteridophyte embryos may be significant in this regard. Furthermore, roots and shoots thus are homologous structures. None of the rooting structures among zosterophylls or lycopods have any kind of emergences or leaves on them except perhaps some fine hairs on those in *Crenaticaulis*. These differ from any ornament on aerial axes. Thus, part of the transformation to a root apex may have been to lose any potential to develop leaves or emergences.

PROTOLEPIDODENDRALES (PROTOLEPIDODENDRACEAE, HASKINSIACEAE, AND
ARCHAEOSIGILLARIACEAE): EARLY LYCOPSID DIVERSIFICATION

Following the Late Silurian-Early Devonian establishment of zosterophylloids and lycopsids, diversification of lycopsids is evidenced by abundant and widespread remains of lycopsids with distinctive anatomical and morphological features. Many of these form a group currently recognized as the Protolepidodendrales. These plants were prominent in Middle to early Late Devonian times and show more advanced and variable leaf morphology and vascular anatomy than pre-lycopsids. Sporangia where known are epiphyllous. Two families and a satellite taxon (Thomas and Brack-Hanes, 1984) are recognized within protolepidodendralean lycopsids.

The Protolepidodendraceae are well known from several parts of the world in Middle Devonian times. They consisted of lycopsids with helically arranged, forked leaves, and globose to elongate sporangia located on the adaxial surface of the leaf. Their characteristic leaves, which are divided into three (*Colpodexylon*, *Minarodendron*) or five or more (*Leclercqia*) segments, are the most striking features of the plants. In many of these taxa, sporophylls resemble vegetative leaves. Sporangia in *Leclercqia* attach by a single discrete layer of cells to the leaf just proximal to its division, and the free part of the sporangium is directed towards the axis. A single line of dehiscence extends the length of the sporangium. Mode of sporangial attachment in other protolepidodendrids is not as clear, but they apparently lack stalks. Permineralized remains of some of these plants show a solid xylem column with several narrow ridges of protoxylem around the periphery (*Leclercqia*, *Minarodendron*), resulting in a shallowly ribbed protostele, or a more deeply lobed xylem strand (*Colpodexylon*). *Leclercqia* is notable for being a ligulate, homosporous taxon (Grierson and Bonamo, 1979). Berry (1996) summarized the considerable new data and major features of these plants and other representatives of the Protolepidodendrales (Table 1).

Pre-Middle Devonian Protolepidodendraceae have been found. Kasper and Forbes (1979) recorded *Leclercqia* sp. from the late Early to Early Middle Devonian of Maine and Kasper (1977) noted the presence of a new species of *Leclercqia* in the Emsian of New Brunswick. In both of these occurrences, axes bear five-segmented leaves, but all segments are oriented in the same direction (Fig. 7B) rather than being three-dimensionally arrayed as in *L. complexa* Banks, Bonamo and Grierson. At the time of recording them, the age determinations of sediments were uncertain. Since then, dispersed spore data indicate the New Brunswick sediments are undoubtedly Emsian. Recent collections from these Emsian New Brunswick outcrops by Gensel document a second occurrence of the genus, these plants being very similar in leaf morphology and sporangial attachment to *L. complexa* (Fig. 7A), differing mainly in their smaller size.

Remains of a plant with leaves possessing a total of nine segments also have been found in the Emsian of New Brunswick. In these forms, four segments are oriented in an upwardly directed, flattened lamina to each side of a long,

TABLE 1. Synopsis of protolepidodendrolean lycopsids.

PROTOLEPIDODENDRALES

- Especially abundant in Middle and early Late Devonian but some occurrences in Emsian (late Early Devonian-shown as asterisk below)
- Plants with dichotomously? branched axes, probably rhizomatous, creeping habit, no leaf scars (leaves persistent); stems protostelic, exarch, xylem with bordered pitted tracheids; leaves inserted in patterns resembling helices or pseudowhorls, sporophylls more or less identical to vegetative leaves, sporangia on adaxial surface of leaf.

PROTOLEPIDODENDRACEAE

*Leclercqia** Banks, Bonamo et Grierson 1972

Minarodendron Li 1990

Colpodexylon Banks 1944

Protolepidodendron Kräusel et Weyland 1932

Leaves divided into up to 9 narrow segments; planate or three-dimensional.

Sporangia elongate ovoid; homosporous where known.

Protostele either lobed (*Colpodexylon*) or denticulate.

HASKINSIACEAE

*Haskinsia** Grierson et Banks 1983 emend Berry et Edwards 1996

Artschaliphyton Senkevich 1971

Leaves petiolate; blade lanceolate, sagittate or hastate.

Sporangia globose to obovoid; spores unknown.

Protostele denticulate.

ARCHAEOGIGILLARIACEAE (satellite taxon)

Archaeosigillaria (Göppert) Kidston 1901

Gilboaphyton Arnold 1937 emend Berry et Edwards 1997

Leaves laminar, with a pair of prominent, lateral, distally oriented 'teeth'; "inflated" hexagonal leaf bases surrounded by subepidermal thickenings.

Fertile structures unknown.

Protostele lobed.

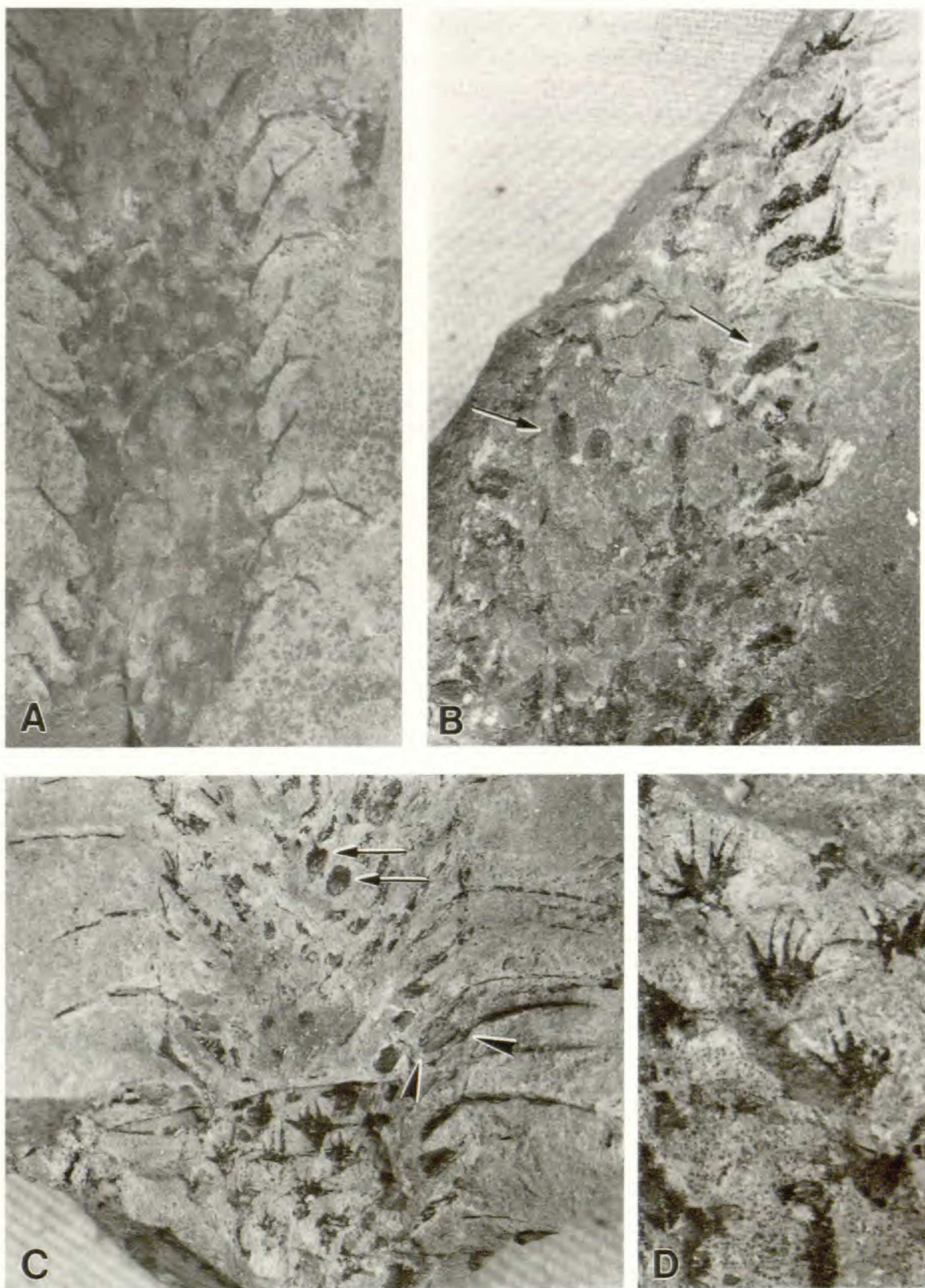


FIG. 7. Illustrations of Protolepidodendraceae from the Emsian of New Brunswick. A) *Leclercqia* collected by Gensel. This is most similar to *L. complexa*, 4X. B) *Leclercqia* sp. described in abstract by Kasper (1974). Oval bodies represent sporangia (arrows). 3.6X. C) New leclercqioid plant with 8-segmented leaf. Note long distal segment, upward trending lateral ones in side view on upper left, an imprint of a sporangium associated with leaf between arrowheads to lower right, other sporangia at arrows, 2.4X. D. New leclercqioid plant with 9-segmented leaf, lateral leaf segments in surface view, 4X.

central, horizontal to downward-extended one (Figs. 7C, 7D). Elongate sporangia attach, perhaps at one end, to the upper surface of the undivided portion of the leaf (Fig. 7C, arrows). Another genus with segmented leaves, *Cervicornus wenshanensis*, was reported from the Pragian of Yunnan, China (Li and Hueber, 2000). This genus has leaves that are divided into two groups of four (eight segments total) segments, arrayed three-dimensionally. Although lacking important diagnostic evidence such as sporangia and anatomy, *Cervicornis* may be the oldest record of Protolepidodendraceae. Thus, more diversification of this group prior to the Middle Devonian is evident. In terms of younger examples, a lycopsid of similar size as all examples of Protolepidodendraceae, and superficially identical in appearance, has been reported from Lower Carboniferous sediments of Argentina. *Frenguella* Arrondo *et al.* (1991) has leaves with a long median segment, and two pairs of shorter opposite lateral tips, two of which point backward towards the stem. Sporangia are borne on unmodified leaves. However, we are concerned about the lack of conclusive and direct evidence for the present dating of these fossils; they may be substantially older.

A second protolepidodendralean type is represented by the Haskinsiaceae (Figs. 8A–8C). This family differs from the Protolepidodendraceae in having more laminate, hastate or sagittate leaves and perhaps in sporangium shape. Leaf morphology varies less within this group than in Protolepidodendraceae. Epiphyllous, globose or flattened ellipsoidal sporangia have been demonstrated in two species of *Haskinsia* from Venezuela, although mode of dehiscence and spores are unknown (Berry and Edwards 1996). *Haskinsia* from New York State has a primary xylem column with peripheral ridges of protoxylem similar to those of *Leclercqia* and *Minarodendron* (Grierson and Banks 1983).

Archaeosigillariaceae, including the genera *Archaeosigillaria* and *Gilboaphyton*, are sometimes regarded as members of the Protolepidodendrales but fertile examples are lacking. *Archaeosigillaria* has recently been restricted to the type specimen (Berry and Edwards 1997). Archaeosigillariaceae *sensu* Berry and Edwards (1997) includes Middle-Late Devonian plants which have a hexagonal pattern of swollen leaf bases on the stem surface, and permanent lanceolate (more or less hastate) leaves (Figs. 8E, 8F). A permineralized specimen of *Gilboaphyton goldringiae* Arnold from Gilboa (Grierson and Banks 1963, Pl. 37, figs 4, 7) demonstrates a protostele with approximately eight peripheral lobes in transverse section. Specimens of *Gilboaphyton griersonii* from Venezuela and New York State have similar leaf bases, and Berry and Edwards (1997) were able to infer the presence of elongate-oval, possibly parenchymatous, regions beneath each leaf base (Fig. 8D). These are suggestive of possible greater differentiation of stem tissue and may represent a prototypical form for one or more types of parenchyma/aerenchyma (e.g. parichnos) associated with leaf traces found in Late Devonian and Carboniferous lycopsids.

Among the Protolepidodendrales, where xylem anatomy is known, secondary wall pitting patterns include simple and bordered pits as well as annular and scalariform pitting. *Minarodendron* tracheids also exhibit pitlet sheets which resemble to some extent pitting found in younger lycopsids, termed

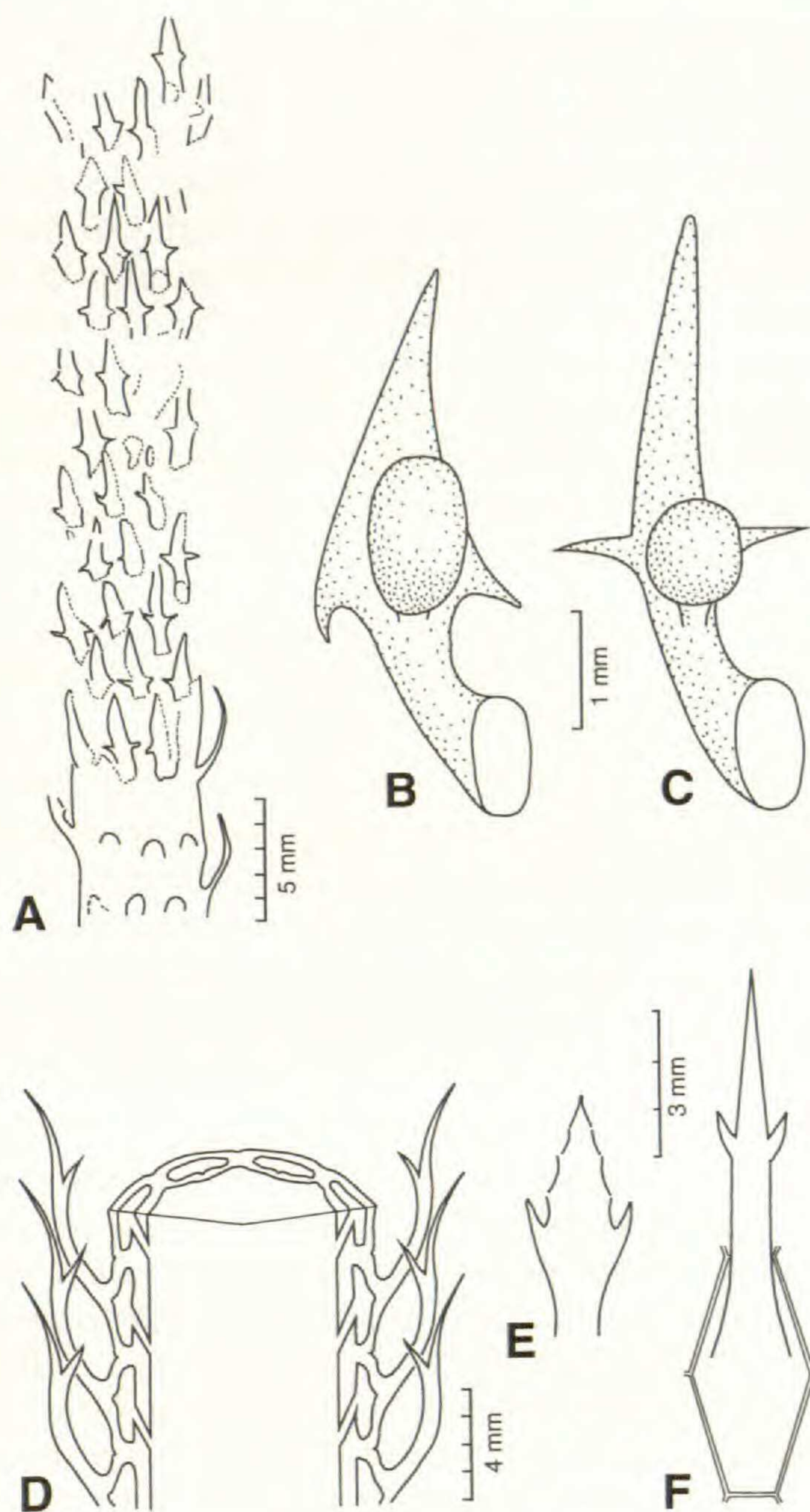


FIG. 8. Haskinsiaceae and Archaeosigillariaceae. A) *Haskinsia*-line drawing of sterile specimen of *H. hastata* from Venezuela. B) Fertile leaf and sporangium of *H. sagittata* Edwards and Benedetto emend. Berry and Edwards from Venezuela. C) Fertile leaf and sporangium of *H. hastata*. D, F) *Gilboaphyton griersonii* from the Devonian of Venezuela. E) *Gilboaphyton goldringiae* from New York State. A—C) Redrawn from Berry and Edwards (1996), D—F) redrawn from Berry and Edwards (1997).

Williamson's striations or fimbriils. Fertile examples, where known, were apparently homosporous. No basal regions or rooting structures have been described. A ligule has been documented only in *Leclercqia*.

Few protolepidodendrolean taxa were included in cladistic studies largely because many of them are not completely enough known. *Leclercqia* and *Minarodendron*, the most completely-known examples, consistently form a clade that is sister, or paraphyletic, to Selaginellaceae or as part of a polytomy with

Selaginellaceae and the rhizomorphic lycopsids (Kenrick and Crane, 1997; Bateman *et al.*, 1992). Further, earlier putative lycopsids such as *Drepanophycus*, *Asteroxylon*, and *Baragwanathia* usually are sister to all of these clades. Most troubling in Protolepidodendrales is our current lack of knowledge about their rooting structures. This feature has the potential to reveal crucial information about relationships of the Protolepidodendrales to other groups, including the arboreous forms. The lack of well-preserved rooting structures is worrisome in the context of the large amount of above-ground material known and the excellence of some of the descriptions. One possible implication is that these plants may not have had specialized rooting structures. Alternatively, rooting structures may have existed, but were not preserved in the same horizons where the stems occur.

INNOVATIONS IN GROWTH HABIT, ROOTING, AND REPRODUCTIVE STRUCTURES IN DEVONIAN LYCOPSIDS

Until recently, the Protolepidodendrales, or certain less well-known remains, were the most likely group from which the Late Devonian and Carboniferous arborescent, ligulate, heterosporous lycopsids may have arisen. A crucial difference between Protolepidodendrales and aborescent forms however, is that the latter have a bipolar shoot system and erect growth habit. New discoveries from China have provided important evidence about changes in growth habit and rooting structures among Devonian lycopsids.

SMALL TREE-LIKE LYCOPSIDS OF THE MIDDLE DEVONIAN.—The earliest examples of true bipolar growth, resulting in upright growth of a trunk and downward growth of a dichotomous rooting system, are to be found in the late Middle Devonian (Givetian) and earliest Late Devonian (Frasnian) of China. The two plants in question are *Longostachys* (Cai and Chen, 1996) and *Chamaedendron* (Schweitzer and Li, 1996). Both are small in height (0.5–1.5m), having a slender trunk that branches isodichotomously at the top to form a crown of narrow branches and terminal cones, and at the base to form a downward-pointing, conical-shaped, rooting system which divides into four major segments (Fig. 9). Roots may dichotomize further but lack any sign of attached rootlets or stigmarian-type rootlet scars.

Longostachys is the larger of the two plants and has secondary growth in both the trunk and the rooting system. Sterile leaves are long and narrow, with spiny margins. Fertile leaves are spoon-shaped (the bowl containing the sporangium nearest the axis), and also have spiny margins (Fig. 9). Both of these plants are interesting because they have major features characteristic of rhizomorphic lycopsids (habit, dichotomous rooting system, bipolar growth) but lack rootlets.

LATE DEVONIAN ROOTING STRUCTURES.—The famous ‘Naples tree’ (*Lepidosigillaria whitei*) from the Late Devonian of New York State has previously been interpreted to have a swollen base covered in stigmarian rootlets (White, 1907; Pigg, 1992, 2001). This specimen is poorly preserved, and suffering pyrite de-

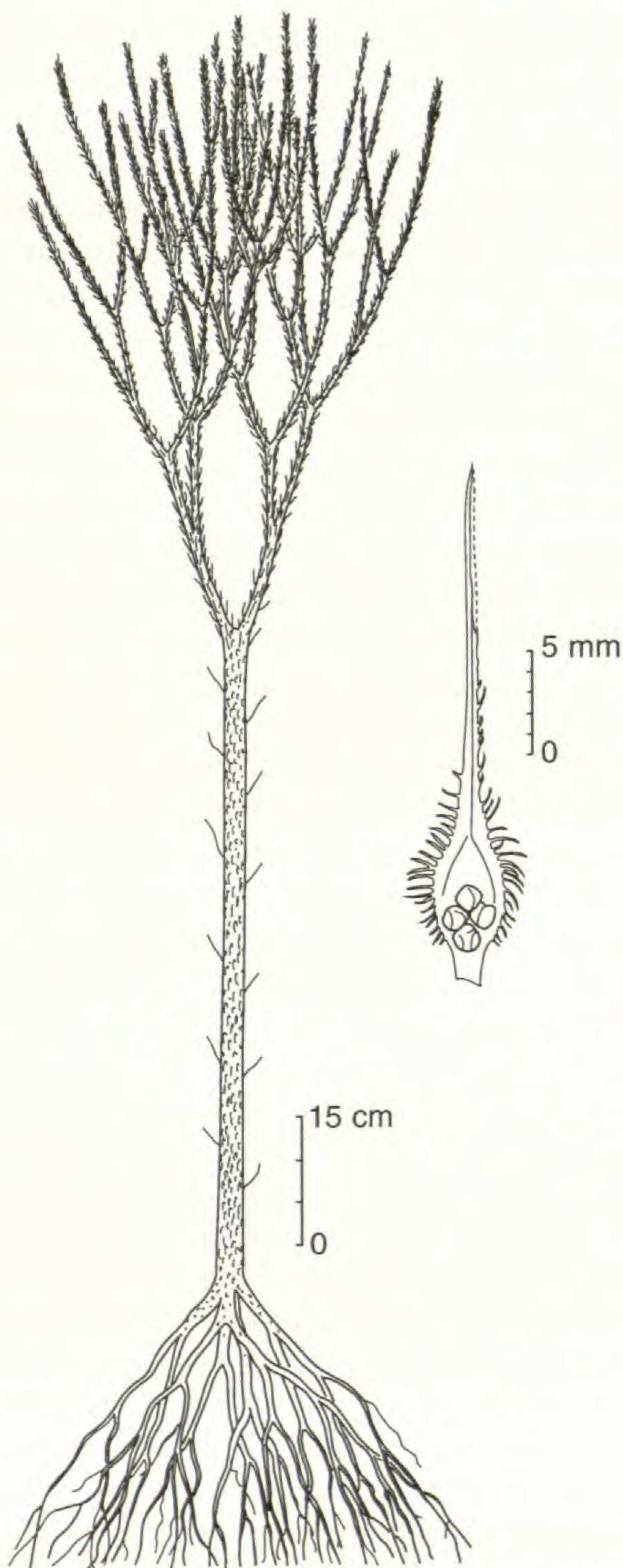


FIG. 9. Reconstruction of *Longostachys*, showing the four-parted rooting structure and leafy stems, and (inset) a single sporophyll. After Cai and Chen 1996, with permission.

cay, and the presence of rootlets and rootlet scars can no longer be verified. The poor quality of White's photographs showing the basal region of the plant compared to his other photographs of the upper trunk would suggest it was no better preserved when he worked on it. Thus we cannot accept this specimen as showing the earliest example of a lycopsid rhizomorph. Earlier Middle Devonian stumps named *Eospermatopteris* (Goldring 1924) which several peo-

ple considered to be possible lycopsid bases (as noted by Pigg, 1992), are far more likely to be cladoxylalean in affinity (Boyer and Matten 1996; Berry and Fairon-Demaret in progress). *Clevelandodendron*, from the Late Devonian (Famennian) Cleveland Shale, has an isoetalean habit but again stigmarian rootlets were not demonstrated (Chitaley and Pigg, 1996). Branched rooting structures are reported, but not described in any detail, for the Upper Devonian *Cyclostigma kiltorkense* (Johnson, 1913). *Leptophloeum* from the Upper Devonian (Famennian) of South Africa has a bulbous base from which many thick dichotomous roots emerge all around (Gess and Hiller 1995). These roots are up to 10 mm wide in comparison with the 45 mm bulbous base width and seem too large to be rootlets. This suggests an absence of rootlets in this plant. Lastly, cormose lycopsid plant bases, some with attached rootlets, have been reported from the Upper Devonian (?late Famennian age) Red Hill, Pennsylvania deposits (Cressler, 1998, 1999; Scheckler *et al.*, 1999).

The previous earliest western occurrence of an undisputed lycopsid rhizomorph (Pigg, 2001) is the report by Jennings *et al.* (1983) of *Protostigmaria eggertiana* from the Mississippian of Virginia, USA. Chinese occurrences include *Stigmaria rugulosa* Gothan from the Upper Devonian Wutung Formation near Nanjing (Gu & Zhi 1974). Berry and Wang Yi collected dichotomous stigmarian roots with characteristic rootlet scars from Nanshan Quarry, in Jiangsu Province, also from the Wutung Formation (unpublished) where other fossils included *Eviostachya* and *Hamatophyton* (Li, Cai and Wang 1995).

The facts, as outlined above, demonstrate that the emergence of the lycopsid rhizomorph remains a mystery. According to Rothwell and Erwin (1985) 'there now can be little doubt that the rooting structures of all rhizomorphic lycophytes are shoot systems modified for rooting' and implied rootlets therefore were homologous to leaves (p. 95). Bateman *et al.* (1992) however recognize that the stigmarian rhizomorph 'is a shoot-like developmental system', but prefer to regard it as a unique organ reflecting limited developmental options within the arborescent lycopsid bauplan'. The new evidence from China suggests that the earliest lycopsids with bipolar growth, although possessing a dichotomous, downwards-pointing rooting system, did not possess stigmarian rootlets, supporting Bateman *et al.*'s hypothesis. Such rootlets are not found until the uppermost Devonian in China and either uppermost Devonian or Lower Carboniferous in the U.S.A.

By the time tree-shaped lycopsids appeared in the Middle Devonian, leaves were well developed as structures, and it seems inconceivable that leaves might have been involved in the development of a downward-directed rhizomorph as implied by Rothwell and Erwin's hypothesis. If the K branching recognized above in zosterophylls and pre-lycopsids (Gensel *et al.*, 2001) does in fact represent the earliest stages of bipolar growth in the Lycophytina (*sensu* Kenrick and Crane 1997) we can propose homologies between structures in zosterophylls and arborescent lycopsids (Fig. 10). In some zosterophylls and in *Drepanophycus*, K-branching occurs, the posterior (or downwards)-directed branch being naked and the apically (or upwards)-directed branch bearing enations or leaves. The two branches are homologous structures, deriving from a

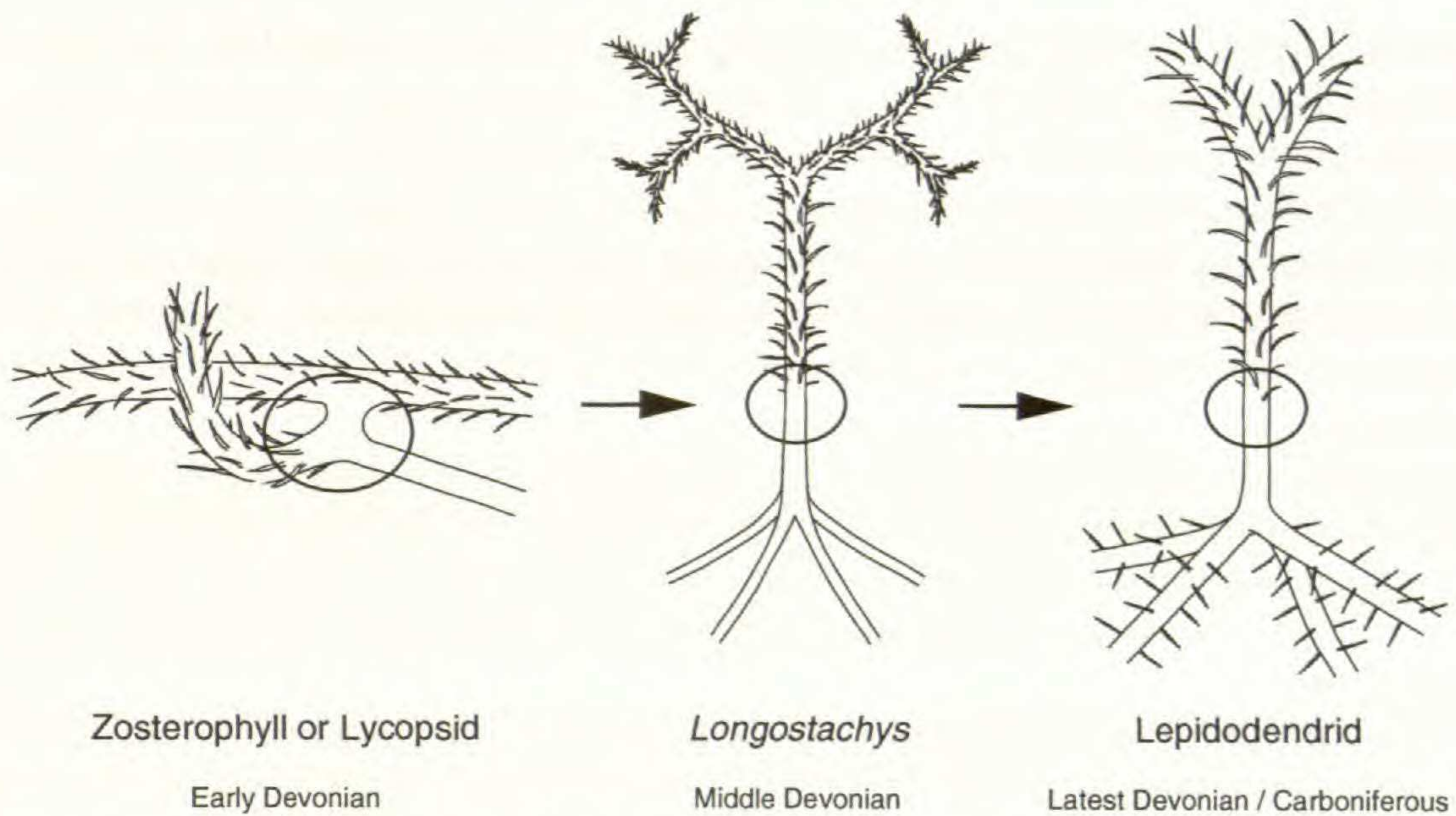


FIG. 10. Hypothesis of homology of rooting structures between creeping early lycophytes (zosterophyll or lycopsid), *Longostachys*, and a Carboniferous arboreous lepidodendrid. Shoot and rooting structures are homologous, being derived by a branching event. Early rooting structures lack lateral appendages; rootlets arose later, possibly in early arboreous forms. See text for further explanation.

regular dichotomous branch as found in all zosterophylls, but the posterior-directed branch having developed the characters of roots and loss of enations/leaves. In the earliest pseudobipolar lycopsids (Middle Devonian of China) the K branching occurs precociously at the initial growth of the sporophyte, causing upward growth of the bifurcate, leafy aerial axes and downward growth of the bifurcate, naked rooting system. Final development of the arboreous lycopsid body plan occurs when rootlets evolve *de novo* on the rooting system to increase efficiency.

INNOVATIONS IN FERTILE STRUCTURES AMONG MIDDLE AND LATE DEVONIAN LYCOPSIDS.—Middle Devonian Protolepidodendrales bear spores in single adaxial sporangia where known. Characteristically the fertile leaves are unmodified compared with the sterile ones. Often this means that the sporangia are borne more or less exposed on narrow leaf pedicels before the leaf forks (e.g. *Leclercqia*, *Colpodexylon*). In Haskinsiaceae, however, the laminate nature of the leaf and its upcurved pedicel (Figs. 8B, C) means that the sporangia are slightly more protected by the leaf (Berry and Edwards 1996). In those Protolepidodendrales where spores are known, the plants are homosporous. Sporophylls are often found concentrated into areas of the axes, but show no closer insertion nor increased overlap to areas of sterile leaves.

In *Chamaedendron*, leaves are slightly broader near their base, but in *Longostachys* sterile leaves are narrow and fertile leaves are distinctly enlarged near their base in the area of attachment of the sporangia (Fig. 9), the shape being suggestive of an upturned spoon. The leaf margins of these Chinese lycopsids are spiny. The enlarged bases of the sporophylls are curved around

sporangia which contain large megaspores, demonstrating that the plant is probably heterosporous (microsporangia are unknown). Leaves are not well enough preserved to know for certain if ligules were present or not. In these small, bipolar, tree-shaped lycopsids the sporophylls are crowded closer together forming distinctive fertile regions, and individual leaves overlap to some extent. Such fertile regions are therefore intermediate between the lax protolepidendrid fertile areas and the compact cones of many more advanced lycopsids.

Lycopsid strobili from Kazakhstan, correlated to the upper part of the Givetian on the basis of plant fossils, are reported to contain a random mixture of mega- and micro-sporangia (Senkevich et al., 1993). These demonstrate an early record of compaction of sporophylls to form a tight, protective strobilus in lycopsids.

A new probably arborescent lycopsid from the uppermost Devonian of Wuxi, China (Berry, Wang, and Cai, in prep), with branches slightly wider than those of *Longostachys*, demonstrates the earliest known occurrence of a lycopsid that has distinct micro- and megasporangiate cone-like structures. Megasporangiate 'strobili' contain leaves similar to those of *Longostachys* (but up to 90 mm long) whereas the microsporangiate strobili contain closely packed sporophylls that are much narrower. The megasporangiate strobili of this lycopsid are not terminal, but occur at dichotomies on the distal axes. Thus some modification and compaction of sporophylls is well underway prior to the end of the Devonian.

CONCLUSIONS

Important new information has been obtained in recent years about the early history of lycophytes, particularly concerning anatomy and morphology of shoots, the occurrence of rooting structures, and greater diversification and differentiation of fertile regions. Recent broadly based phylogenetic analyses of vascular plants present interesting hypotheses of relationships, the most significant result being recognition of zosterophylloids, lycopsids, and of several basal lineages not yet well known. These analyses increase our understanding of lycophytes, zosterophylloids and lycopsids as natural groups, but do not at this stage help significantly to clarify relationships within and between these groups. Moreover, some characters and possibly character states employed in these phylogenetic studies require modification or re-interpretation in order to more fully resolve relationships. For example, the phylogenetic positions of several plants more traditionally viewed as zosterophylls remain unresolved as do the relationships of presumed basal lycophytes from China which show extremely interesting combinations of characters. Interpretation and understanding of important morphological characters and character-state transformations which appear to be critical in delineation of major clades are presently particularly unsatisfactory, and remain a major obstacle to resolution of early lycophyte phylogeny. Important examples include helical versus linear insertion of sporangia, presence/absence of circinate vernation, and inter-

pretation of sporangial shape, orientation, and mode of dehiscence. Re-evaluation is also particularly needed in linking early lycopsids (?protolapidodendrids) to the bipolar, increasingly arborescent Late Devonian/Carboniferous forms. Although we can view a simple transformation sequence of, for example, the Middle Devonian protolapidodendrolean fertile leaf via the Middle / Upper Devonian *Longostachys* sporophyll to the compacted Carboniferous cone, we do not see a corresponding pattern in the evolution of the stigmarian rooting system using the conventional homologies of rootlets and leaves. With dramatic advances in our knowledge of fossils as likely in the next decade as has occurred during the past three decades, and perhaps better understanding of the developmental basis for evolutionary change, we anticipate greater understanding of the early radiation of lycophytes in the years to come.

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